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# The role of the vibration signal during queen competition in colonies of the honeybee, *Apis mellifera*

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Temporary polygyny (the presence of multiple queens) occurs in honeybee colonies when virgin queens (VQs) are reared for reproductive swarming or queen replacement. During these events, workers perform vibration signals on queen cells and emerged queens, and these signals may influence which VQ becomes the new laying queen of a colony. We examined the role of vibration signals during queen competition in two African and six European honeybee colonies. There was pronounced variability in vibration activity between colonies and among queens reared within the same colony. Despite this variation, all colonies showed similar trends in the relationships between the vibration signal and queen replacement. Vibration signals performed on queen cells were not associated with emergence success. Likewise, the signal was not associated with queen emergence order. Early emerging and late-emerging queens were vibrated at similar rates, and there was no clear relationship between emergence order and VQ survival. However, the signals performed on VQs after they emerged were associated with their behaviour and success during the queen elimination period. Emerged VQs that were vibrated at higher rates survived longer, performed more bouts of piping (a characteristic sound produced by queens), eliminated more rivals and were more likely to become the new queens of the colonies. The vibration signal may therefore allow workers a degree of control over the behaviour of emerged VQs, and may influence the outcome of queen competition in honeybees. Differences in vibration activity within and among colonies may reflect differences in the extent to which workers and queens conflict over the timing and outcome of polygyny reduction.



Reproductive conflict has a major impact on shaping animal social behaviour and may be particularly important in the highly social insects (Hastings et al. 1998; Bourke & Chan 1999; Bourke & Ratnieks 1999; Reeve 2000). An extreme example of reproductive conflict occurs in the honeybee, *Apis mellifera*. Although colonies are normally monogynous (containing only one queen), temporary polygyny occurs during reproductive swarming and emergency queen rearing. During these events, multiple virgin queens (VQs) are reared within specially constructed queen cells. Once emerged, some VQs may depart in afterswarms with portions of the workers (Fletcher & Tribe 1977; Winston 1987). More typically, however, VQs attempt to destroy unemerged 'rivals' still within queen cells and battle other emerged queens to the death. The end result is a single surviving VQ that becomes the new laying queen of the colony. The outcome of polygyny reduction has a pronounced impact on colony survival and worker inclusive fitness. Mechanisms for influencing queen elimination may therefore be under strong selection and may provide insights into the factors that regulate honeybee social organization (Tarpy et al. 2000).

Polygyny reduction in honeybees is dependent in part upon queen fighting ability. The factors affecting fighting success are poorly understood, but may include: (1) body size and weight (Hatch et al. 1999), (2) pheromonal signals (Bernasconi et al. 2000), (3) emergence order, because early emerging VQs may have more opportunities to eliminate rivals still within queen cells (DeGrandi-Hoffman et al. 1998), and (4) 'piping' behaviour, which consists of a VQ producing a series of pulsed sounds that may advertise her fighting ability and inhibit the emergence of rivals (Bruinsma et al. 1981; Grooters 1987; Visscher 1993). However, it is unlikely that overt fighting alone determines the outcome of queen replacement. Worker honeybees may exert a strong influence on the

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requeening process by destroying developing queen cells, inhibiting queen emergence and preventing emerged VQs from fighting (Tarpy & Fletcher 1998; Hatch et al. 1999). Indeed, worker influences could potentially be the primary determinants for the outcome of reproductive conflict and queen elimination (Visscher 1993; Tarpy et al. 2000). However, little is known about the role of workers during temporary polygyny in honeybees (Hatch et al. 1999; Tarpy et al. 2000), or in most other species that show polygyny reduction (Heinze 1993; Keller & Vargo 1993; Adams & Balas 1999; Bernasconi & Strassmann 1999).

A mechanism by which honeybee workers may influence queen behaviour is the 'vibration signal', which consists of a worker rapidly vibrating her body dorsoventrally for 1–2 s, while grasping a queen cell or a VQ with her legs (Allen 1959). Although queen cells and VQs can be vibrated hundreds of times an hour, the rates at which individual queens receive the signal can vary tremendously (Fletcher 1978b; Painter-Kurt & Schneider 1998b). Workers may therefore preferentially direct vibration activity toward certain VQs. However, the function of the signal during temporary polygyny is unclear. Vibration signals performed on queen cells may inhibit emergence (Fletcher 1978b; Bruinsma et al. 1981). Those performed on emerged VQs may affect locomotion and piping activity (Fletcher 1978a; Schneider 1990, 1991), which could influence encounter rates with rivals and aggressive interactions. The vibration signal may therefore provide a valuable tool for investigating the role of workers in reproductive conflict during temporary polygyny. However, there has been little systematic study of how the vibration signal might affect VQ emergence, postemergence behaviour and fighting success.

This study investigated vibration signal activity during queen rearing and polygyny reduction. We had three main objectives. First, we examined the association between vibration signals performed on queen cells and emergence success (e.g. whether the cell produced an emerged VQ or was destroyed before emergence). Second, we explored the possible interactions among emergence order, the vibration signal, and the ability of VQs to survive the elimination period. Third, we examined the relationships between vibration signals performed on emerged VQs and their postemergence behaviour and fighting success.

## METHODS

### Study Sites and Study Organisms

We report the combined results of three separate studies that investigated vibration signals during queen replacement. The first study was conducted by S.S.S. in 1986 on two colonies of the African honeybee, *A. m. scutellata* (colonies A1, A2), in the Okavango River Delta, Botswana, Africa. The second study (conducted by S.S.S. and S.P.-K. in 1996) examined two colonies of European bees (E1, E2) on the campus of the University of North Carolina, Charlotte, North Carolina, U.S.A. The third study (conducted by S.S.S. and G.D.-H. in 1999) investigated four colonies of European honeybees (E3–E6), monitored at the Carl Hayden Honey Bee Research Center, Tucson, Arizona, U.S.A.

In all three studies, colonies were housed in glass-walled observation hives. The Okavango study utilized two-frame observation hives maintained inside high-walled canvas tents (see Schneider 1991 for details of African colony maintenance). The North Carolina and Arizona studies utilized four-frame observation colonies kept indoors in climate-controlled rooms (see Painter-Kurt & Schneider 1998a for details of European colony maintenance). The entrances of all observation hives abutted openings cut into the walls of the tents or rooms to allow free flight to and from the colonies. The walls of the observation hives were marked off in grids of 5 $cm^2$ to facilitate monitoring queen cells and VQs. When necessary, the glass walls of the observation hives were replaced with Plexiglas sides that contained hinged access ports through which VQs could be marked with distinguishing colours of paint. Otherwise, queens were distinguished based on natural variations in cuticular colours.

The two African colonies examined in the Okavango raised VQs in association with reproductive swarming. Each of these colonies occupied its observation hive for at least 1 month before queen rearing and swarming preparations were initiated. The European colonies monitored in North Carolina and Arizona were forced to undergo emergency queen replacement by removing the laying queen after each colony had occupied an observation hive for at least 1 week. Colonies E1 and E2 swarmed during the queen replacement process. Because the two swarms contained virgin queens, they were classified as afterswarms (Fletcher & Tribe 1977; Winston 1979).

### Monitoring Queen Cells and Emerged Queens

During the swarming and queen replacement periods, we checked colonies six to eight times each day. Every developing queen cell was given an identification number and its location was marked on the glass walls of the observation hive. Data collection began once the first queen cell was sealed in a colony. We then scanned colonies continuously for 30-min periods, four to eight times each day, and recorded the number of times each queen cell was vibrated. Subsequently, we calculated a vibration rate for each queen cell, by dividing the total number of vibration signals observed by the total number of 30-min observation periods. We also recorded the 'emergence success' of each queen cell by noting if a cell produced an emerged VQ or was destroyed before emergence.

As the queen cells neared emergence (indicated by a thinning of the cells' wax cappings), we began monitoring the colonies continuously for at least 8–10 h each day, and frequently for 24 h/day. Whenever possible, observations were conducted by two observers so that both sides of the hives could be monitored simultaneously. For each queen, we recorded the cell from which she emerged, the time of her emergence, and the paint mark she received or her individual colour markings. Each VQ was identified according to her emergence order (i.e. the first queen

to emerge was identified as VQ1, the second as VQ2, etc.). Each VQ was then monitored continuously (subdivided into 30-min periods) throughout the time she was present in the colony. We recorded for each queen the total number of vibration signals received and subsequently calculated her vibration rate per 30-min period. We also recorded the total bouts of 'piping' performed and determined the piping rate per 30-min period. Additionally, we determined for each queen (1) the number of emerged VQs she eliminated through combat; (2) the number of unemerged queen cells she destroyed; (3) the total number and proportion of rivals eliminated (emerged VQs plus queen cells); (4) her 'fate' (whether she became a laying queen or was killed); and (5) the duration of her presence in the colony (in hours). We assigned to each new laying queen a survival time of 336 h, because each was still present in the colonies 14 days after emergence, at which time the studies were terminated. Virgin queens that left with afterswarms were also assigned a survival time of 336 h.

### Determining the Influence of Vibration Signals on Emergence Success

We compared vibration rates between cells from which VQs emerged versus those that were destroyed before emergence. We conducted these comparisons using repeated measures analysis of variance (ANOVA), which used colony as the subject and had one within-subjects factor (emergence success) and one between-subjects factor (race).

### Assessing the Relationships Among Emergence Order, the Vibration Signal and VQ Survival

We used two approaches to examine the interactions among emergence order, the vibration signal and queen success. First, we used Spearman rank correlation analysis to examine the associations among a VQ's emergence order, the rate at which she was vibrated while in her queen cell, the vibration rate experienced after she emerged, and her postemergence survival time. We performed the correlation analyses separately for each race.

Second, we examined whether being the first VQ to emerge conveyed a survival advantage, and whether first emergence was associated with the rate at which queen cells and VQs were vibrated. For each colony, we noted whether the first VQ to emerge became the new laying queen or was killed by a rival. We used repeated measures ANOVA to compare the first-emerged queen to all other VQs in her colony, with respect to the vibration rates received while in the queen cells and after emergence.

### Determining the Association between the Vibration Signal and VQ Behaviour

We also used two approaches to examine the relationships between the vibration signal and the postemergence behaviour and success of VQs. First, we used Spearman rank correlation analysis to examine the associations among piping rates, survival times, proportion of rivals eliminated and the vibration rates experienced after emergence for all VQs. We determined these correlations separately for the African and European VQs. We also calculated the correlations using only the data for those VQs of each race that were killed. In this manner, we were able to assess if any observed trends applied across all queens, or resulted primarily from the few successful VQs that were assigned a survival time of 336 h.

For our second approach, we conducted a more detailed investigation of postemergence behaviour by comparing surviving queens to those that were killed during polygyny reduction. We used repeated measures ANOVA to compare surviving versus killed VQs with respect to (1) postemergence vibration rates (2) piping rates, and (3) the proportion of rivals eliminated.

We observed enormous differences in vibration signal production among the different colonies, and especially between the two races (see Results). As a result, comparisons of actual vibration rates in the repeated measures ANOVA yielded main effects and interaction terms that were often difficult to interpret. In particular, using the raw data for the very high vibration rates for the African queens in the ANOVAs resulted in highly significant differences between the two races that may have masked any trends exhibited within the European colonies. However, comparisons between the races were necessary to determine whether the African and European colonies displayed similar trends, regardless of the actual levels of vibration activity. We therefore standardized our data by calculating for each queen cell and VQ a 'relative vibration rate', defined as the rate experienced by an individual cell or VQ divided by the mean rate experienced over all cells or queens within a colony. We also calculated relative piping rates to adjust for the large differences in piping activity observed among queens (see below). We then conducted our analyses of variance using these relative rates. This method revealed the same trends found when using the raw data, but eliminated the highly significant racial differences. Thus, we report the results based on the relative rates to allow for more interpretable comparisons. We used the raw data for the correlation analyses, because each race was examined separately.

Because our data were not normally distributed, we transformed the data prior to conducting the analyses of variance. We used a square-root transformation to normalize the data for relative piping rates; a fourth root transformation normalized the data for relative vibration rates. Proportional data were arcsine transformed (Sokal & Rohlf 1995). All statistical tests were two tailed and the sequential Bonferroni adjustment (Rice 1989) was used to determine significance levels for the multiple comparisons made among colonies and between races. All mean values are reported as $\pm 1$ SE.

## RESULTS

The two African colonies produced a total of 10 queen cells in association with swarming, of which seven

**Table 1.** The total number of queen cells produced, the number that emerged, those that were destroyed before emergence, and the mean±SE number of vibration signals performed/30-min period on the cells in each study colony

| Colony | Total cells | Emerged cells | Destroyed cells | Vibration signals per 30-min period |
|---|---|---|---|---|
| African | | | | |
| A1 | 3 | 2 | 1 | 65.2±31.7 |
| A2 | 7 | 5 | 2 | 181.3±33.2 |
| European | | | | |
| E1 | 32 | 12 | 20 | 1.45±0.30 |
| E2 | 32 | 19 | 13 | 0.97±0.21 |
| E3 | 7 | 4 | 3 | 0.07±0.04 |
| E4 | 20 | 2 | 18 | 0.02±0.01 |
| E5 | 10 | 1 | 9 | 0.09±0.04 |
| E6 | 5 | 3 | 2 | 0.07±0.06 |

emerged and three were destroyed before emergence (Table 1). These 10 cells received 146.5 ± 29.9 vibration signals per 30-min period (Table 1). The seven emerged VQs received 198.0 ± 65.0 vibration signals/30-min period, produced 17.2 ± 10.3 bouts of piping/30-min period, and eliminated 28.6 ± 14.4% of their rivals (Table 2). Three of the African VQs survived the elimination process; two became the new laying queens of the colonies and the third left with an afterswarm from colony A2. The remaining four VQs were killed within 15.3 ± 9.0 h of emergence (Table 2).

The six European colonies produced a total of 106 queen cells in association with emergency queen replacement, of which 41 emerged and 65 were destroyed before emergence (Table 1). The 106 cells received on average less than one vibration signal per 30-min period (Table 1). We obtained complete data records for 25 of the 41 emerged European queens (Table 2). Of the remaining 16 VQs, three were found dead before data could be gathered and 13 emerged within a 24-h period in colony E2 immediately following an afterswarming event. The extreme activity associated with the presence of this large number of queens made it impossible to monitor individual activity reliably, and these 13 VQs were not included in the analyses of postemergence behaviour. The 25 VQs for which complete records were available received 9.5 ± 3.9 vibration signals/30-min period and eliminated 23.9 ± 7.1% of their rivals (Table 2). Piping was monitored in colonies E3–E6 and these observations revealed a mean piping rate of 0.4 ± 0.1 bouts/30-min period (Table 2). Seven of the 25 monitored European VQs survived the elimination process; six became the new laying queens of the colonies and one left with an afterswarm from colony E1. The remaining 18 VQs were killed within 18.1 ± 6.0 h after emergence (Table 2).

There was tremendous variability in vibration activity among the study colonies. In particular, the vibration rates observed for the African colonies were far greater than those observed for the European colonies (Tables 1, 2). However, there was also marked variability between the different European colonies (Table 2), and vibration rates on the different queens within the same colony varied dramatically. All eight study colonies produced at least one VQ that received no vibration signals, while other queens received 2–472 signals/30-min period. These differences in vibration activity within and between colonies, plus the observed differences in VQ survival time and behaviour (Table 2), suggested a possible association between the signal and queen success.

## Vibration Rates and Emergence Success

We found no relationship between the rate at which queen cells were vibrated and emergence success. The mean relative vibration rate on the cells from which queens emerged did not differ from that observed for cells destroyed before emergence (ANOVA: $F_{1,6}$=1.21, $P$=0.313; Fig. 1). This trend did not differ between the two races and there was no race-by-emergence success interaction (ANOVA: NS for both comparisons).

## Emergence Order, Vibration Rates and Virgin Queen Survival

We found no consistent associations between emergence order, the vibration signal and postemergence survival. For the African VQs, there was no correlation between a queen's emergence order and the rate at which she was vibrated while in her queen cell (Spearman rank correlation: $r_S$=0.436, $N$=7, $P$=0.328). In contrast, the European VQs showed a significant, positive correlation between emergence order and the vibration rate experienced while in the queen cells (Spearman rank correlation: $r_S$=0.495; $N$=25; $P$<0.05). Thus, in the European colonies the more a cell was vibrated the later its VQ emerged during the rivalry period. However, there was no correlation between emergence order and postemergence vibration rates experienced by either the African VQs (Spearman rank correlation: $r_S$=0.266, $N$=7, $P$=0.564) or the European queens ($r_S$= − 0.299, $N$=25, $P$=0.146). Similarly, there was no association between emergence order and survival time for either the African ($r_S$= − 0.048, $N$=7, $P$=0.92) or European VQs ($r_S$= − 0.339, $N$=25, $P$=0.10).

Being the first queen to emerge also was not consistently associated with survival or the vibration signal. The first queen to emerge became the new laying queen in four of the colonies (A1, E4, E5 and E6), while in the remaining four the first-emerged VQ was killed. The mean relative vibration rate on the queen cells that emerged first (0.78 ± 0.13 signals/30-min period) did not differ from that of the later-emerging cells (0.94 ± 0.06 signals/30-min period; ANOVA: $F_{1,5}$=0.43, $P$=0.238). Likewise, the postemergence vibration rates experienced by the first-emerging queens (0.96 ± 0.15 signals/30-min period) did not differ from that of the later-emerging VQs (0.59 ± 0.12 signals/30-min period; ANOVA: $F_{1,5}$=2.03, $P$=0.213). Thus, early emergence was neither clearly influenced by the rate at which queen cells were vibrated, nor did it affect the vibration rates or survival success experienced by VQs after emergence.

**Table 2.** The number of surviving and killed VQs that were monitored in the study colonies, and the mean±SE vibration signals received/30 min, bouts of piping performed/30 min, and proportion of rivals eliminated by each

| Colony | Surviving VQs | Killed VQs | Vibration rate | Piping rate | %Rivals eliminated | Survival time (h) for killed VQs |
|---|---|---|---|---|---|---|
| African | | | | | | |
| A1 | 1 | 1 | 137.9±123.8 | 0.0 | 50.0±50.0 | 0.5 |
| A2 | 2 | 3 | 219.7±80.0 | 24.1±13.5 | 20.0±11.0 | 20.2±10.7 |
| European | | | | | | |
| E1 | 2 | 9 | 19.3±8.1 | NR | 9.1±4.1 | 18.1±10.2 |
| E2 | 1 | 4 | 1.9±1.4 | NR | 19.4±15.0 | 28.5±12.8 |
| E3 | 1 | 3 | 1.4±0.6 | 0.4±0.1 | 25.0±0.2 | 14.0±9.6 |
| E4 | 1 | 1 | 0.3±0.0 | 0.2±0.2 | 50.0±50.0 | 3.5 |
| E5 | 1 | 0 | 3.3 | 0.3 | 100 | DBE |
| E6 | 1 | 1 | 2.9±2.1 | 0.6±0.4 | 50.0±50.0 | 3.5 |

Mean survival times are given for the killed queens. Piping was not recorded (NR) in colonies E1 and E2. All rivals in colony E5 were destroyed before emergence (DBE) by the one emerged VQ.

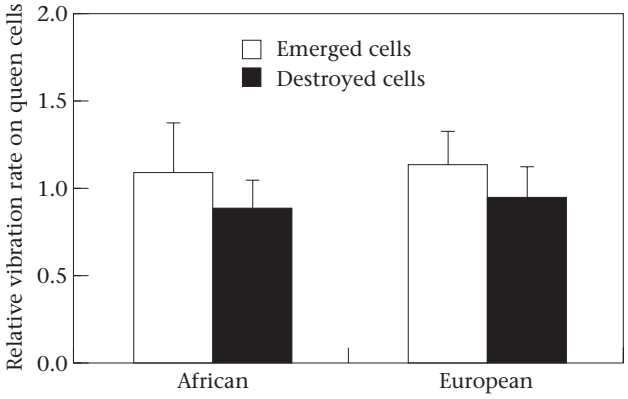


**Figure 1.** The mean±SE relative vibration rate experienced by queen cells from which a VQ emerged versus those that were destroyed before emergence in the African and European colonies. We calculated the relative rate for each cell by dividing its vibration rate by the mean rate experienced over all cells within the colony.

## Vibration Rates on Virgin Queens and Postemergence Success

The correlation analyses revealed three main relationships between the rates at which VQs were vibrated and their postemergence survival and behaviour. First, in both African and European colonies, VQ survival times were significantly and positively correlated with the vibration rates experienced after emergence (Table 3). Queens that survived less than three hours were never vibrated, while those that lived longer typically began to receive the signal within one or two hours of emergence. Second, in both races the proportion of rivals eliminated was significantly and positively correlated with the vibration rate experienced by a VQ (Table 3). Third, piping rates were positively correlated with VQ vibration rates, although this association was not significant for the African queens (Table 3). Thus, despite the pronounced differences in vibration activity, both races exhibited the same trend: higher vibration rates on VQs were associated with longer survival times, greater fighting success and (in the European colonies) increased piping behaviour.

**Table 3.** Coefficients for the Spearman rank correlation between vibration rates on VQs and the different aspects of their survival and behaviour examined by race for all queens and those killed by rivals

| Correlation of VQ vibration rate with: | African colonies | | European colonies | |
|---|---|---|---|---|
| | All VQs (*N*=7) | Killed VQs (*N*=4) | All VQs (*N*=25) | Killed VQs (*N*=18) |
| Survival time (h) | 0.812* | 1.00* | 0.606* | 0.812* |
| %Rivals eliminated | 0.925* | 0.816 | 0.596* | 0.615* |
| Piping rate | 0.299 | 0.778 | 0.732*† | 0.918*† |

*$P$<0.05, based on the sequential Bonferroni adjustment.
†$N$=9.

These correlations persisted when examining only those VQs that were killed by rivals. In both the African and European colonies, there was a significant, positive correlation between survival time for the eliminated rivals and vibration rate experienced (Table 3). Thus, even if a queen was eventually killed, the length of time she was present in the colony was associated with the number of vibration signals she received per 30-min period. VQs that were killed also showed positive correlations between the proportion of rivals eliminated, piping rate and vibration rate, although these relationships did not reach significance in the African colonies because of small sample sizes (Table 3). The observed trends therefore occurred across all VQs and did not arise primarily from the behaviour of the few queens that survived polygyny reduction.

The comparisons of surviving versus killed VQs also suggested an association between the vibration signal and queen success. Compared to the queens that were eliminated, the surviving VQs were vibrated at higher relative rates (ANOVA: $F_{1,5}$=10.12, $P$=0.0245; Fig. 2), had greater relative piping rates (ANOVA: $F_{1,5}$=20.38, $P$=0.020; Fig. 3), and eliminated a greater proportion of rivals (ANOVA:

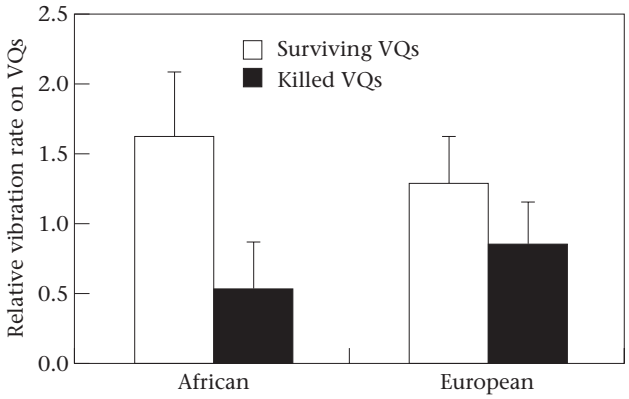


**Figure 2.** The mean±SE relative vibration rate experienced by surviving versus killed queens in the African and European colonies. We calculated the relative rate for each VQ by dividing the vibration rate she personally experienced by the mean rate experienced over all queens within her colony.

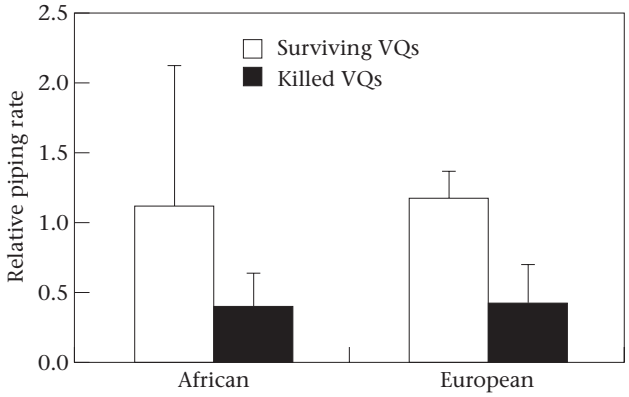


**Figure 3.** The mean±SE relative piping rate for surviving versus killed queens in the African and European colonies. For the European queens, piping was monitored for the nine VQs that emerged in colonies E3–E6. We calculated the relative rate for each VQ as her personal piping rate divided by the mean rate over all queens within her colony.

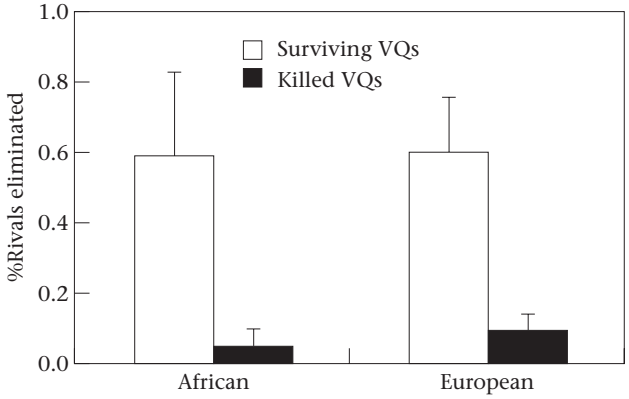


**Figure 4.** The mean±SE proportion of rivals eliminated by surviving versus killed queens in the African and European colonies.

$F_{1,5}$=15.71, $P$=0.0107; Fig. 4). These trends did not differ between the African and European colonies, and there were no race-by-fate interactions (ANOVA: NS for all comparisons). The comparisons of the surviving and killed queens were therefore consistent with the correlation analyses. Both approaches suggested that, regardless of the actual level of vibration activity, the two races showed the same basic relationship between the signal and queen behaviour: higher vibration and piping rates were associated with greater success during the rivalry period.

## DISCUSSION

Our results suggested that during temporary polygyny, virgin honeybee queens that were vibrated at higher rates relative to their rivals piped more, survived longer, experienced greater fighting success, and were more likely to become the new queens of the colonies. Vibration signals performed on queen cells did not consistently influence VQ emergence. The signal may therefore allow workers a degree of control over the behaviour and interactions of queens once they emerge, and this could occur in at least two ways. The signal may promote contact and fighting among VQs, because it elicits greater movement throughout the nest (Allen 1959; Schneider 1991). However, most available evidence suggests that the signal inhibits queen interactions (Fletcher 1978b; Schneider 1991). In particular, vibrated VQs often respond with brief bursts of running (Schneider 1991) that could remove them from potential battles and temporarily prevent fighting. Either way, the signal may give workers some ability to influence queen aggression and potentially represents a mechanism of worker–queen conflict during polygyny reduction.

The correlative nature of our data does not necessarily suggest a cause-and-effect relationship between the vibration signal and queen success. The signal might enhance the survival of queens that are vibrated at higher rates, perhaps by delaying their interactions until they have greater maturity and fighting ability. Alternatively, the signal could be used to protect less-vibrated VQs from opponents, which might be vibrated at higher rates to temporarily thwart their attacks. At present, we do not know whether queens have more success specifically because they are vibrated at higher rates, or if they are vibrated more in response to their inherently greater fighting abilities.

We observed enormous variation in vibration activity between and within colonies. This variation could be a starting point for interpreting the role of the signal during reproductive conflict. If the signal impedes VQ aggression, then vibration activity should be greater in situations of increased worker–queen conflict. Visscher (1993) hypothesized that conflict would be more pronounced in swarming colonies, because workers and VQs may conflict over which queens should leave with afterswarms and when rival elimination should occur. Indeed, we observed the highest vibration rates in three of our four colonies that produced primary swarms or afterswarms during requeening (Tables 1, 2). Thus, the level of vibration activity may be context dependent and vary with the degree to which workers and queens follow different strategies for reproductive success.

The different vibration rates experienced by VQs within the same colony suggest that workers preferentially direct their signalling activity towards certain queens. Such discriminations could be based on cues that reflect relatedness (Tarpy & Fletcher 1978), reproductive capacities (Tarpy et al. 2000), or VQ size and fighting ability (Grooters 1987; Hatch et al. 2000; Bernasconi et al. 2000). However, at present we do not know to what extent, if any, these factors influence vibration rates on VQs, and in particular we do not understand fully the reasons for the much greater vibration activity observed for our African queens. Experimental manipulations of queen quality will be necessary to tease apart the factors that influence vibration signal performance during queen elimination.

Queen cells that were vibrated at higher rates in our European colonies tended to emerge later. Fletcher (1978b) and Bruinsma et al. (1981) also observed an association between the signal and delayed emergence, but Grooters (1987) did not. No relationship between the vibration signal and emergence order was observed for the African cells in our study. Regardless, emergence order in the present study had little association with postemergence survival. Our results therefore suggest that it is primarily the interactions between the vibration signal and postemergence behaviour that ultimately affects VQ success during queen elimination.

Influencing queen interactions is probably not the sole function of the vibration signal during temporary polygyny. VQs can be vibrated at high rates more or less continuously for days, and it seems unlikely that such continuous signalling would be necessary to regulate only occasional interactions. The vibration signal may function as a 'modulatory signal' that can affect multiple activities by a recipient simultaneously, depending upon contextual cues (Schneider 1987; Nieh 1998; Beshers et al. 1999; Lewis & Schneider 2000). Signals performed on VQs may therefore allow workers to influence not only rival interactions, but also mating flights and the onset of oviposition (Allen 1959; Fletcher 1978a; Schneider 1990, 1991). Vibration-like signals are widespread among social insects and in several species may influence queen behaviour during polygyny reduction (West-Eberhard 1978; Schneider et al. 1986; Painter-Kurt & Schneider 1998b). Such signals may therefore provide an important mechanism for investigating worker–queen interactions in a variety of species for which temporary polygyny is a part of the colony cycle.

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